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AN EXPLANATION OF VISUAL ADAPTATION IN ACCORDANCE WITH THE SPECTRAL SCANNING THEORY

By

George Biernson

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SECTION 1

IMPLICATIONS OF SPECTRAL SCANNING IN VISUAL ADAPTATION

This memorandum extends the Spectral Scanning theory[1]
of color vision to include visual adaptation. It shows that
the theory provides a new approach to this phenomenon, which
has many important implications in the science of color vision.
If we accept the Spectral Scanning theory, we are led to the
conclusion that the main aspects of chromatic and achromatic
adaptation would be performed prior to the demodulation pro-
cess that generates the trichromatic signals. In other words,
visual adaptation would be performed in terms of the spectral
pattern information, as represented by the spatial energy
distributions, and the modulated waveforms produced by scanning
the spatial energy distributions. Since the spectral pattern
information is more than three dimensional, the Spectral Scan-
ning theory represents a multi-dimensional theory of color
vision. This is in direct contrast to the classical three-
dimensional concept of color vision embodied in the Trichromatic
theory.

Let us clarify what we mean by dimensionality. A spec-
trum of light may be considered as having infinite dimensions,
because an infinite number of values are theoretically required
to define the spectrum exactly. For example, one can des-
cribe a spectrum by specifying its values at every wavelength,
and a great number of wavelengths are required for accurate
specification of certain spectra. Each wavelength can be
considered mathematically as representing a dimension in multi-
dimensional space, and the value of the spectrum at a given
wavelength is the coordinate for that dimension.

According to the most common version of the Trichromatic
theory, the retina has three types of cones, each having a dif-
ferent photopigment. Each cone is sensitive only to the rela-
tive power of the spectrum of the incident light weighted by

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the absorption spectrum of the pigment in the cone. A single cone therefore generates a one-dimensional visual signal, and the combination of the signals from the three cones forms a three dimensional color signal.

In contrast, the Spectral Scanning theory postulates that the infinite dimensional light spectrum is converted by the waveguide mode effect to form a spectral pattern, which is then processed in the performance of visual adaptation. The processed spectral-pattern information is finally demodulated to generate the three-dimensional color signals. Because of the limited wavelength resolution of the waveguide mode effect, the spectral pattern is not infinite dimensional, but it undoubtedly has a dimensionality much higher than three.

The implementation of visual adaptation in terms of multi-dimensional spectral patterns can allow considerably greater accuracy of spectral discriminations than would be achievable if adaptation were performed in terms of three dimensional color signals carried in separate channels. Natural chemical feedback processes associated with photopigment bleaching can translate the light from an object into a spectral pattern that accurately describes the ratio of the spectrum of the object to the time average spectrum that the cone has received. Assuming that this time average spectrum represents the spectrum of the illuminant, the chemical feedback thereby compensates for the spectrum of the illuminant and generates a spectral pattern corresponding directly to the reflectivity spectrum of the object.

Multi-dimensionality in the spectral pattern would assure that very small variations in spectra would produce detectable differences in spectral patterns for wide ranges of illuminant spectra and object reflectance spectra. This would allow the eye to detect with high accuracy very small amounts of chromaticity in the reflectiority spectrum of an object, and very small differences in the reflectivity spectra of two neighboring objects.

Thus the Spectral Scanning theory provides a basis for a new theoretical approach to the visual adaptation process. This approach appears to have the potentiality of explaining quantitatively how the eye is able to achieve such great fidelity of interpreting the reflectivity spectra of objects in an invariant manner, as the illuminant is varied over great ranges of intensity and chromaticity.

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SECTION 2

ACHROMATIC VISUAL ADAPTATION PROCESS

Chromatic adaptation can be best understood by considering first the achromatic adaptation processes. Various feedback processes are required to adjust the characteristics of the receptors so that they are kept in accurate calibration while the visual system adjusts to different light intensities.

One of the key factors in visual adaptation is the continual motion of the eye over the field of view. This consists of small involuntary motions that the eye cannot control plus the larger motions of the eye that are under voluntary control. This motion allows the separate receptors to become individually adapted to the average background illumination, and is an important factor in keeping the visual system in calibration.

This motion of the eye can be eliminated by artificially stabilizing an image on the retina, moving the image to compensate for eye motions.[2,3] When this is done the image fades out in less than a minute, chromatic and achromatic sensations fading out simultaneously.

The primary mechanism associated with the slowly varying aspects of visual adaptation is the bleaching of the photopigments in the receptors. When a photon of light is absorbed by a photopigment molecule, the molecule is immediately isomerized (i.e., its physical configuration is changed). This initiates a chemical process that results in the bleaching of the molecule.[4]

There is a regeneration process that converts the bleached molecules back to photopigment molecules. The rate of regeneration is proportional to the concentration of bleached molecules. If the incident light is removed (so that there is no bleaching) the concentration of bleached molecules is reduced to 37 percent in a time measured by Rushton[5,6,7,17] to be about 2 minutes for cones and 10 minutes for rods. This time will be called the regeneration time constant τ_r.

The eye adapts to a given illumination as follows. The incident light bleaches the pigment molecules, causing the concentration of bleached molecules to increase. The greater the concentration of bleached molecules, the faster the molecules are regenerated. Therefore an equilibrium state is eventually reached at which the bleached molecules reaches the concentration for which the regeneration rate is equal to the rate of bleaching by the light.

When a pigment molecule is bleached, it appears likely that the chemical process produces some form of charge differential which generates a flow of current. Since regeneration is the reverse process electrically to bleaching, it is a reasonable hypothesis that the regeneration of a molecule of photopigment produces a current that is equal and opposite to that produced by bleaching a molecule of photopigment. Thus the photopigment region would act as a balanced detector which delivers as an output the difference between the currents produced by bleaching and regeneration. Under equilibrium conditions the bleaching and regeneration currents are equal, and no net current is delivered. Raising the light intensity produces an excess of bleaching current, and an output current of one polarity is produced. Lowering the light produces an output current of opposite polarity.

This concept of a balanced detector is consistent with Hering's postulate that the eye has a black-white opponent-process substance. For a grey object the receptor delivers no signal, because this represents the equilibrium condition. A white object delivers more light than the average and so produces a signal of one polarity, whereas a black object delivers less light than the average and so produces an opposing signal.

From a psychological point of view it is very desirable that the black sensation is produced by a signal generated directly in the optical detection process, because black is

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just as real a color sensation as are the other basic colors; white, blue, yellow, green, and red. However, Dr. F. Dimmick pointed out to the author that there is also a seventh color sensation, grey, that should be included in the color theory.

The sensation of grey could result from the way the color data is transmitted along the optic nerve to the brain. It appears likely that the neural signals of an opponent pair of colors are sent in a balanced fashion down two optic nerve fibers. One fiber fires when the stimulating light is turned on, and so transmits the white signal, while the opposing fiber fires when the light is turned off, and so gives the black signal. There is a low quiescent firing level in all nerve fibers which would tend to obscure the signal. However, if the brain subracted the outputs from the two opposing nerve fibers the quiescent firing rates would tend to cancel out, and a high resolution black-white opponent signal would be produced. The brain may also be sensitive to the sum of the two signals from the two nerve fibers and this sum signal could give rise to the grey sensation.

Thus the concept of a grey sensation is consistent with the Spectral Scanning theory, but would be produced by neurological processes that follow the receptor. The receptor itself would initiate only the six opposing color sensations, white, black, blue, yellow, green, and red.

The opposing current due to regeneration that has been hypothesized would produce shot noise because of the discrete nature of the electron flow. The author calculated this shot noise and determined from it the visual threshold that it would produce for various concentration of visual pigment.[8] He found that this agreed with measured data taken by Baker[9] within a factor of two, which is within the accuracy of certain assumptions required in the author's calculation. This data represented the visual thresholds of the rods measured 2 seconds after the start of dark adaptation: after the neurological transients had ended, but before there was significant change in the concentration of bleached pigment.

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Thus there is good evidence to substantiate the balanced detector hypothesis. Without this hypothesis there does not appear to be any good explanation of the relationship between visual threshold and photopigment concentration. This is an important point, because as well be shown the balanced-detector assumption is a very important element in the explanation of the visual adaptation process.

An important factor to consider in explaining visual adaptation is the tremendous dynamic range of the retina. The eye has a dynamic range of about 100 decibels, i.e., the maximum light intensity that can be safely tolerated is 10^{10} times larger than the minimum detectable light intensity. The iris varies the light intensity by a factor of 16. Bleaching of molecules reduces the effective light intensity, because the quantum efficiency is proportional to the concentration of photopigment. However, this reduction in quantum efficiency is significant only at high intensities, and has a maximum reduction of about 8. Thus the iris and bleaching change the effective light intensity by a factor of 128, or somewhat more than 20 decibels. Since the total dynamic range of the eye is about 100 decibels, the ratio of maximum to minimum incident power that is effectively absorbed is 10^8 (or 80 decibels).

Each photon that is effective bleaches one molecule of photopigment. Hence the maximum rate of molecular bleaching in a receptor is 10^8 times greater than the minimum rate of bleaching. Since bleaching in some way generates an electrical current, one can consider that the receptor has an input current that varies over the fantastic range of 10^8 to one.

The optic nerve has a very low dynamic range, because it sends messages to the brain coded in terms of a pulse rate. Since the number of quanta of information that can be supplied depends on the time interval chosen, it is difficult to define the dynamic range of the optic nerve. However, one can conservatively estimate that the dynamic range of a nerve fiber is no greater than 100 to one. Since the input current to the

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retina varies by a factor of 10^8, there must be a compensatory gain change of one million to one (i.e., 10^6) in the retina.

Part of the million-to-one gain change is probably achieved by the manner in which the signals from the receptors are integrated together in the bipolar cells. However, there can be little doubt that a very large part of this gain variation must be achieved within the receptors themselves. The requirement that the receptors achieve accuracy of calibration over this very large variation of gain is an important constraint in the possible operation of the visual adaption process.

In this discussion we have ignored for the purpose of simplicity the differences between rods and cones with respect to this adjustment of gain. While these effects are important they do not alter the general conclusions.

How are the separate receptors kept in calibration with one another as the gains are adjusted over such a large range? It seems essential that each receptor have some form of feedback control of gain. The feedback loop should have a very long time constant so that the variations from receptors to receptor are not erased by the feedback loop. It appears logical that this feedback loop should have a time constant roughly equivalent to the time constant of photopigment regeneration, which is 2 minutes for cones and 10 minutes for rods. This idea that the receptors have a slow feedback loop to control their individual gains has been previously proposed by Boynton.[10]

There is good reason to believe that there are other factors that assist in the control of the gains of the individual receptors. It is very difficult for a single feedback loop to achieve the very large change of gain that is required, and so it is likely that the receptors use an additional gain adjustment technique to make the task simpler for the feedback loop.

The most important factor in a gain-control operation is the information used to control the gain. The receptor might control its gain as a function of the concentration of bleached pigment, the higher the concentration the lower the gain. However, it is difficult to see how the bleached pigment concentration itself could be conveniently measured to control the gain. An alternative hypothesis is that the receptor is able to detect the regeneration current independently of the bleaching current and uses the value of the regeneration current to control the gain. Since the regeneration current is proportional to the concentration of bleached pigment, its value would have the same effect in the control.

Another possibility is that the receptor is able to sense the sum of the bleaching and regeneration currents, and uses this sum to control the amplifier. As will be shown there is strong reason to believe that this is what is done. However, it is simpler to describe the adaptation process if the regeneration current alone is used for gain control, and so this will be assumed in the detailed discussion of the system.

Figure 1 gives a block diagram showing a possible means by which the gain and bias of an individual receptor could be controlled. This diagram may not be completely accurate, but it probably gives at least a reasonable first approximation of the actual system.

The incident light P_i (expressed in photons per second per receptor) is multiplied by the quantum efficiency $\eta(\lambda)$ to give the effective photon rate per receptor. The efficiency η varies with wavelength λ in proportion to the scopic luminosity curve for the rods and in proportion to the photopic luminosity curve for the cones. The maximum efficiency is about 0.1 for rods and is probably about the same for the cones. The difference in sensitivity of the cones and rods at low light intensities appears to be caused by (1) the inherent noise level in the cones being about 14 times that of the rods and (2) the integration area of the rods being about 50 times that of the cones.[7]
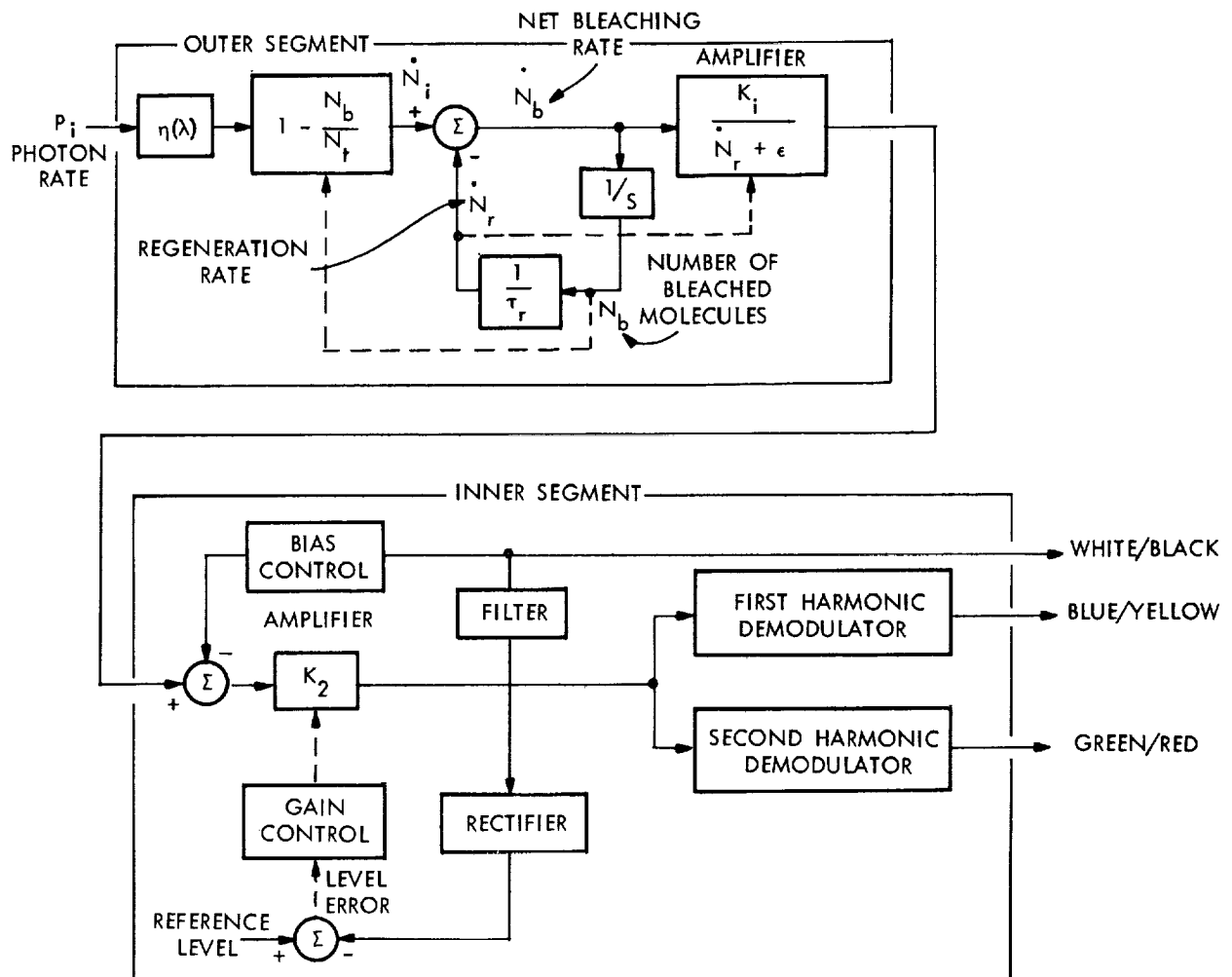
Figure 1. Possible System For Controlling Gain and Bias of Individual Receptor

The effective quantum efficiency varies in proportion to the concentration of photopigment. This effect is indicated by the factor $(1 - N_b/N_t)$, where N_b is the number of bleached pigment molecules and N_t is the total number of pigment molecules, unbleached plus bleached. Under normal lighting conditions the concentration of bleached pigment is quite small. It is only at very high intensities that this factor $(1 - N_b/N_t)$ departs significantly from unity, and it has a minimum value of about 1/8 at maximum light intensity.

The rate of bleaching of photopigment molecules by the light is indicated as $\dot{N}_i$ and the rate of regeneration of the photopigment molecules is indicated as $\dot{N}_r$. The difference between these two rates is the net rate of change of bleached molecules $\dot{N}_b$, which defines the net signal developed in the balanced detection process. The number of bleached molecules N_b is the time integral of the net bleaching rate $\dot{N}_b$. This integration action is represented in the block diagram by the LaPlace transform operator (1/s) by the expression

$$N_b = (1/s)\dot{N}_b \qquad\qquad (1)$$

In a non-rigorous sense the LaPlace operator (s) may be considered to be equivalent to the differential operator (d/dt). The regeneration rate is related to the concentration of bleached pigment by

$$\dot{N}_r = N_b/\tau_r \qquad\qquad (2)$$

where τ_r is the regeneration time constant. Rushton has measured τ_r to be about 10 minutes for rods and 2 minutes for cones.

It seems essential that there be some amplification process in the outer segment because of the tremendous dynamic range and sensitivity of the receptor. If the receptor is to use information concerning the concentration of bleached pigment, or

the regeneration current, to control its gain (which appears to be necessary for effective control), it is logical that it would be the gain in the outer segment that is controlled by this information. Thus the block diagram shows a variable gain element in the outer segment represented by the transfer function $K_1/(\dot{N}_r + \varepsilon)$. This would approximately vary the gain inversely with the regeneration rate $\dot{N}_r$, producing high gain at maximum dark adaptation when the regeneration rate is low and low gain under light adaptation conditions. The small factor ε is added to $\dot{N}_r$ in order to keep the gain from becoming infinite when $\dot{N}_r$ is zero.

Another possibility is that the receptor uses for gain control the sum of the magnitudes of the regeneration and bleaching currents, which is proportional to $(\dot{N}_r + \dot{N}_b)$. The amplification transfer function would then be $K_1/(\dot{N}_r + \dot{N}_b)$. The signal E delivered by the outer segment would be

$$E = K_1 \left[\frac{\dot{N}_b - \dot{N}_r}{\dot{N}_b + \dot{N}_r} \right] \tag{3}$$

For convenience let us consider a normalized signal X equal to E/K_1. Now the bleaching rate $\dot{N}_b$ is proportional to the instantaneous input light power P_i, and the regeneration rate $\dot{N}_r$ is proportional to the average value P_o of the input light power. Hence the normalized signal X delivered by the outer segment can be represented as

$$X = \left[\frac{P_i - P_o}{P_i + P_o} \right] \tag{4}$$

This control relation has the important advantage that the normalized signal X never exceeds the limits of ± 1. It has a value of zero for a neutral grey object, a value of -1 for a completely black object, and never exceeds +1 for the brightest white object. Thus the control keeps the signal within a fixed operating range of the receiver.

Yilmaz[11] theorized that in order for an individual to per-
ceive object colors essentially independently of changes of
the spectrum of the illuminant the chromatic adaptation process
must approximately follow a transformation law of the form
of the Lorentz transformation of Special Relativity. The same
line of reasoning would lead one to predict that the achromatic
adaption process to different light intensities should also
follow a Lorentz   Transformation. It can be shown that the
control law represented in Eq. (4) corresponds to a Lorentz
transformation in perceptual coordinates.

We can relate the normalized signal X given in Eq. (4)
to the brightness sensation B by assuming that as the sensation
varies from -1 to +1 the brightness varies from 0 to 10. Thus
our brightness parameter would be comparable to Munsell value.
By Eq. (4) the resultant expression for B would be

$$B = 5(1 + X) = \frac{10\ P_i}{P_i + P_o} \tag{5}$$

This is the same expression derived by Adams and Cobb[12,13] in
1922 to show the effect of an adapting luminance P_o on the
apparent brightness of an object of luminance P_i.

Thus it appears that there is strong evidence that Eq. (4)
defines the proper gain control law of the receptor. However,
it is simpler to discuss the adaptation process in terms of
the assumption that the regeneration rate alone is used for
gain control, as was indicated in Figure 1. Since the quali-
tative results are quite similar the simpler assumption will
be employed.

Let us return to Figure 1. The signal delivered by the
outer segment is fed to the inner segment where it is amplified
by the gain K_2 to form the receptor output signal. This output
is filtered to form the white-black (or luminosity) informa-
tion and demodulated to form the blue-yellow and green-red
chromaticity signals. To adjust the gain K_2 the output is
rectified, probably by a full wave rectifier, and the average
rectified signal compared with a reference level. The error

in output level, averaged over the control-loop time-constant (probably about 2 minutes for cones and 10 minutes for rods), is fed back to control the gain K_2 in such a manner as to reduce the error in level to zero.

Since the receptor acts as a balanced detector, it would have an output of essentially zero if there were no drift in the amplification process. However, because of the tremendous gain, the amplification processes would drift considerably unless appropriate measures were taken. One method of eliminating drift is to a-c couple the amplification stages, so that there is no signal transmission at zero frequency. The difficulty with this approach is that the time constant of the coupling network would have to be comparable or greater than the regeneration time constant, which is several minutes. Another approach is to feed back the average output through a slow bias control loop as is indicated in Figure 1. This feedback loop must also have a long time constant but it may be convenient to achieve it by chemical feedback means.

With the adaptation processes illustrated in Figure 1, the retina could slowly adapt to any fixed illumination level and keep the receptors in accurate calibration and optimized to work at that level. However it cannot correct for fast adaptation changes. Measurements made by Baker[8] show that when a background light of 984 trolands is suddenly turned off, the threshold drops by a factor of 25 in 0.2 seconds to a final threshold that is equivalent to a continuous light of 5 trolands.*

What produces this rapid change of threshold? One postulate is that it is achieved by data processing in the neurons which follow the receptors. The argument against this is that the dynamic range is so great. The adaptation level (984 trolands) is about 200 times that of the threshold after turning

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*The threshold was measured by means of a flash of light of 0.02 seconds. Since the integration time of the receptors is 0.1 seconds the short flash of light is equivalent to a continuous light of one-fifth its intensity.

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off the adapting light (5 trolands). With the adapting light
turned on, a light intensity many times greater than the
adaptive level could be carried without saturating the visual
system, or affecting the state of adaptation. Thus the ratio
of maximum to minimum light intensity is much greater than
1000 to 1. To achieve this performance without changing the
gain in the receptors when the light is turned off would
require that the receptors and following neurons have a tre-
mendous linear range, which seems very unreasonable.

This argument leads to the conclusion that some form of
fast feedback control is used to change the gain in the recep-
tors in order to produce this rapid 25-to-1 increase in sensi-
tivity after the adapting light is removed. How can this be
achieved? The logical argument is that the outputs from the
receptors are directly summed together to form weighted average
signals which are used in feedback loops to control gain and
bias in the receptors. These feedback loops would produce
the primary effects of simultaneous contrast.

Figure 2 gives a block diagram showing a possible des-
cription of how the fast feedback loops might work. The block
diagram of the outer segment of the receptor is the same as
that shown in Figure 1, and so is not shown. The rectified
outputs from the various receptors are summed together to
form an average rectified signal which is fed back in a fast
feedback loop to control the gain. The luminosity signals from
the various receptors are summed in a similar summing network
and fed back to control the bias.

Let us see how the receptor would respond to turning off
the light if it were controlled as indicated in Figure 2.
Initially the receptors are nearly balanced in output. When
the light is turned off the outer segments are unbalanced and
deliver a strong negative current that drives the inner seg-
ment amplification into saturation. If the threshold is meas-
ured at this instant it would be higher because of the satura-
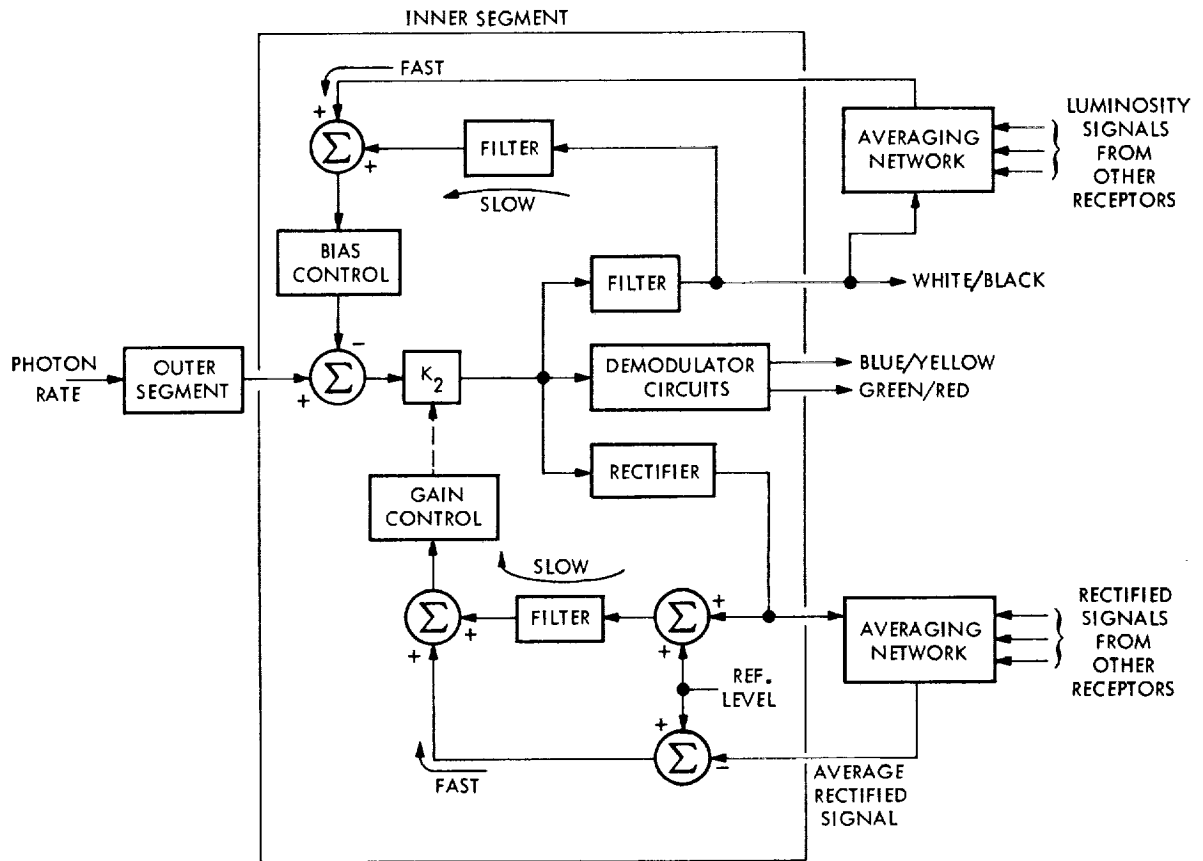tion effect. Soon, however, the bias feedback loop takes over.

Figure 2. Possible Feedback Circuits For Providing Simultaneous Contrast and
Callibration of Receptors

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It compensates for the unbalance and brings the signal back into the center of the amplification range. The gain control increases the gain in the inner segment, which results in a drop in threshold.

The final value of threshold, which is reached a second or two after turning off the light, is established by the noise produced in the regeneration process.[8] When the adapting light is on, the threshold is evidently established by the noise level in the neurons that follow the receptors. Turning the adapting light off, would allow the receptor gains to be increased, which would reduce the relative effect of noise in the following neurons. This would cause the threshold to drop to the value established by shot noise in the pigment regeneration current.

Baker[9] has made measurements of the threshold levels during early dark adaptation, and these are in agreement with the operation described above of the postulated gain and bias control system for the receptors.

On the basis of straightforward systems arguments a model has been developed of the achromatic adaptation processes of the receptors which appears to be consistent with experimental data. Although this model is probably inaccurate in certain details, it should serve as a good first approximation. Let us now generalize this model so that chromatic adaptation is performed, and examine how well it satisfies our knowledge of the chromatic adaption process.

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SECTION 3

CHROMATIC ADAPTATION

The achromatic visual adaptation model can be generalized
to perform chromatic adaptation by making the following assumptions:

(1)   The regeneration current and gain control process in
      outer segment are localized effects that occur prior
      to the scanning process.

(2)   The fast feedback loops in the inner segment that
      control gain and bias are sufficiently fast to follow
      the modulation of the waveform produced by the scanning
      process.

As will be shown, applying these assumptions to the achromatic
adaptation model provides a very simple and effective explanation
of chromatic adaptation.

Figure 3 shows how the sequential-contrast effects of chro-
matic adaptation would be produced by the action of bleaching
in the receptor. Diagram (A) represents the energy density as
a function of position across the cone for what will be assumed
to be the background illumination. This light will generate the
bleaching current density shown as curve (1) in Diagram (B). If
the receptor were initially adapted to a light have a flat spectrum,
curve (1) would define the output signal from the cone.

As the cone adapts to the illuminant, the bleached pigment
builds up in accordance with the pigment density shown in Diagram
(C). This produces a regeneration current density shown as curve
(2) in Diagram (B). The regeneration current density (2) subtracts
from the bleaching current density (1), to produce a net current
density (3) which is zero. Thus the net output current from the
receptor has been reduced to zero with adaptation.

If the adapting light were turned off, the regeneration
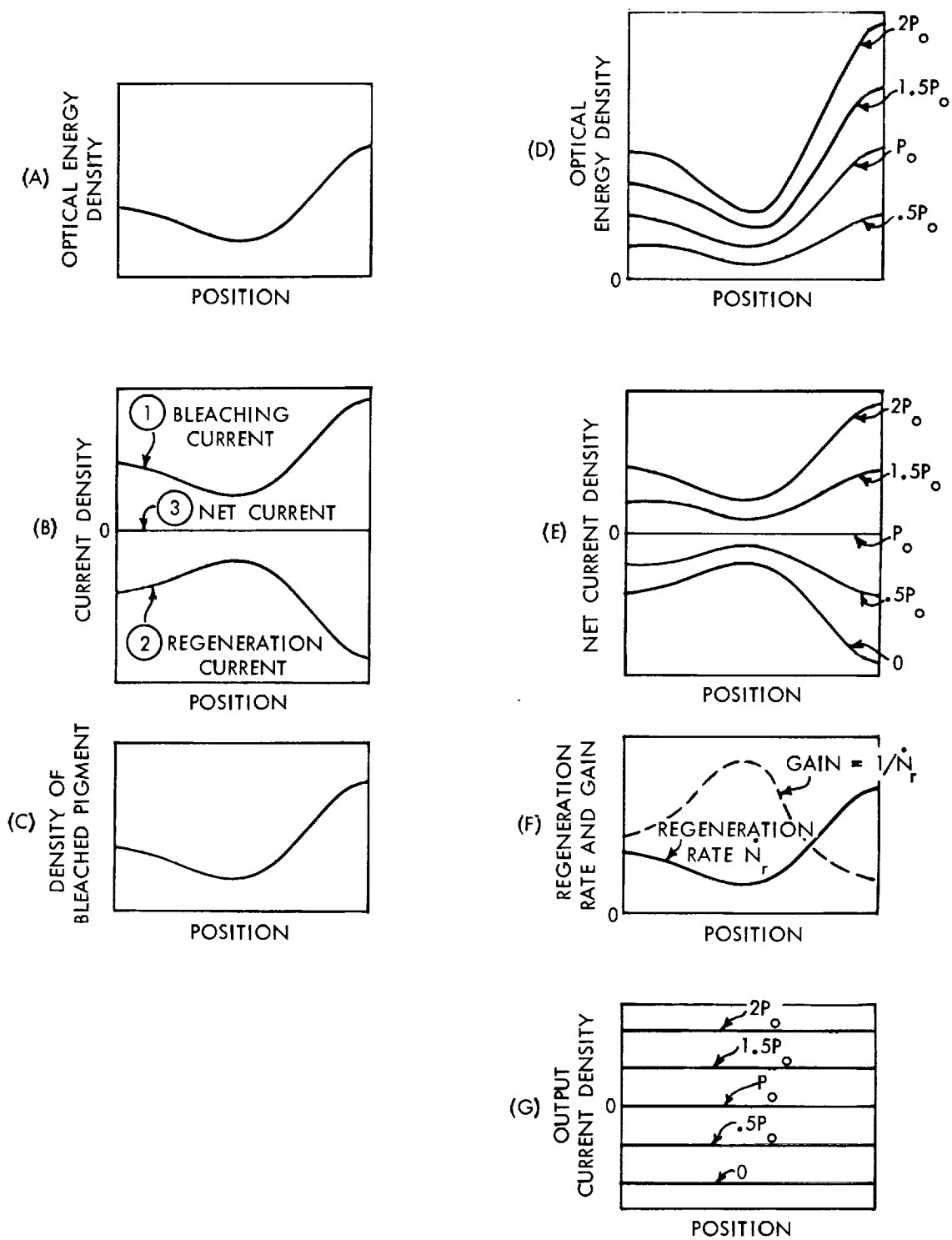current (2) would be the net current. This has the opposite

Figure 3.   Effect of Sequential Color Contrast

spatial variation to that of the adapting illuminant, and so would give a signal corresponding to the complement of the illuminant color. This effect is responsible for complementary after images.

Let us assume that the eye is in a completely achromatic situation, so that the spectra from the various objects vary only in intensity. The intensities are assumed to be 0, 0.5 P_o, P_o, 1.5 P_o, and $2P_o$, where P_o is the average illumination intensity to which the cone has become adapted. Diagram (D) shows the energy densities across the cone produced by the light from the five objects. Diagram (E) shows the net current densities produced in the cone. For the average illuminant the net current density is zero as it was in Diagram (B). For the black object of zero light intensity the net current density is the regeneration current that was given as curve (2) in Diagram (B).

Diagram (F) gives a plot of the regeneration rate $\dot{N}_r$, which is the magnitude of the regeneration current (2) shown in Diagram (B). Now Figure 1 shows that the gain in the amplification process is adjusted to be proportional to $1/(\dot{N}_r+\varepsilon)$ or approximately to $1/\dot{N}_r$. If we assume that there is localized amplification across the cone, the amplification gain would vary across the cone as shown by the dashed $(1/\dot{N}_r)$ curve in Diagram (F).

If we multiply the current density curves of Diagram (E) by the gain plot in Diagram (F), we get the output current density curves shown in Diagram (G). It is these curves that define the signal generated by the scanning process. Since all the curves are flat, the receptor would deliver constant signals for all the five objects. Thus all the five objects would appear achromatic, which is what is required. The effect of bleaching in the outer segment constantly adapts the cone so that an object with the same spectrum as the average spectrum will appear achromatic.

In the above dicussion we chose a gain control that is proportional to $(1/\dot{N}_r)$ rather than a more likely gain control

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that is proportional to $1/(N_r+N_i)$. If the latter gain control were used, the results would be the same except that the vertical spacings between the constant curves of Figure 3G would be varied. The effect would be to compress the curves for intensities greater than unity so that the maximum positive and negative variations of the output current density would be equal (i.e., the normalized output current would always be within the limits of -1 and +1).

If the background illumination should suddenly change, the outer segments would no longer be adapted to the average illuminant and so modulated signals would be delivered from achromatic objects. This effect is compensated for by the simultaneous contrast effects performed by the fast feedback loops in the inner segments, so that the net signals delivered by the receptors are not modulated.

Figure 4 illustrates the chromatic adaptation action produced by simultaneous contrast. Let us assume that the eye is initially adapted to a flat energy density curve which produces the bleaching current density shown by Curve (2) in Diagram (A). The regeneration current would then be curve (3). Now let us assume that the average bleaching current is changed from curve (2) to curve (1). The net output current density from the receptor for an average intensity object would change from zero to curve (4).

Diagram (B) shows the current densities that would occur for our five achromatic objects. The curve for P_o is the same as Curve (4) in Diagram (A), and the curve for zero intensity (the black object) is the same as curve (3) of Diagram (A).

When the field scans back and forth across the cone the five current densities of Diagram (B) generate the five modulated waveforms shown in Diagram (C). These signals are fed into the inner segment where they are amplified.

The signal from all the receptors are fed into a summing network to form an average signal.. If the eye is looking over a balanced field of view, the average signal from the receptors will correspond to the average intensity P_o. Thus the average
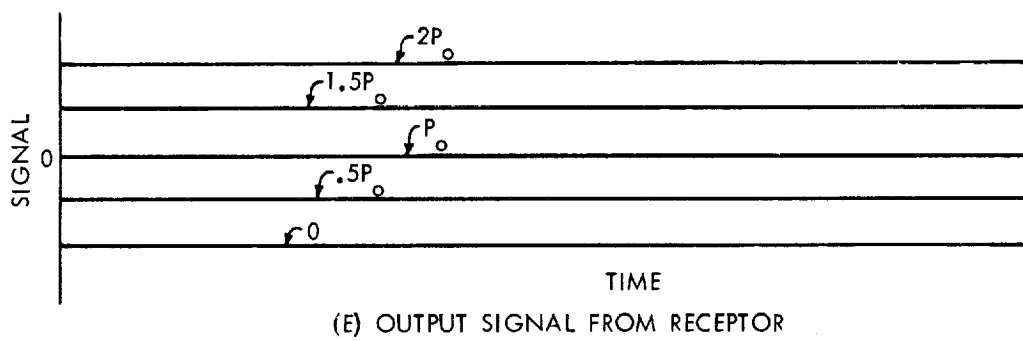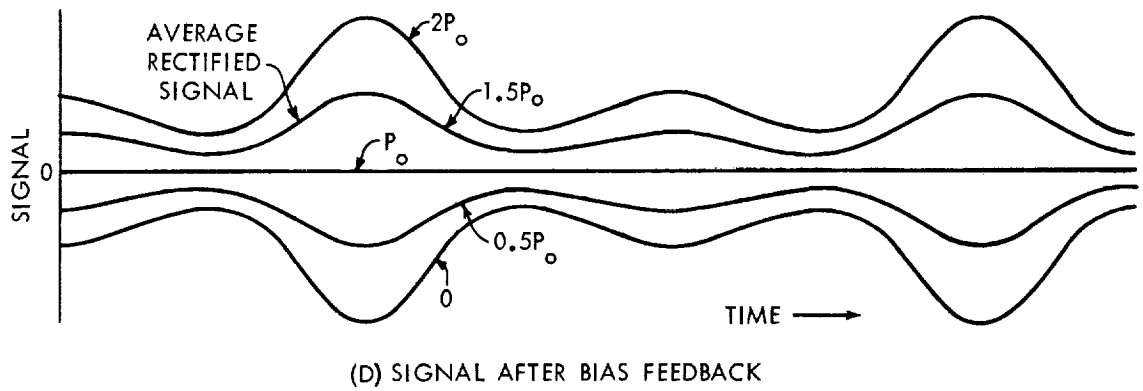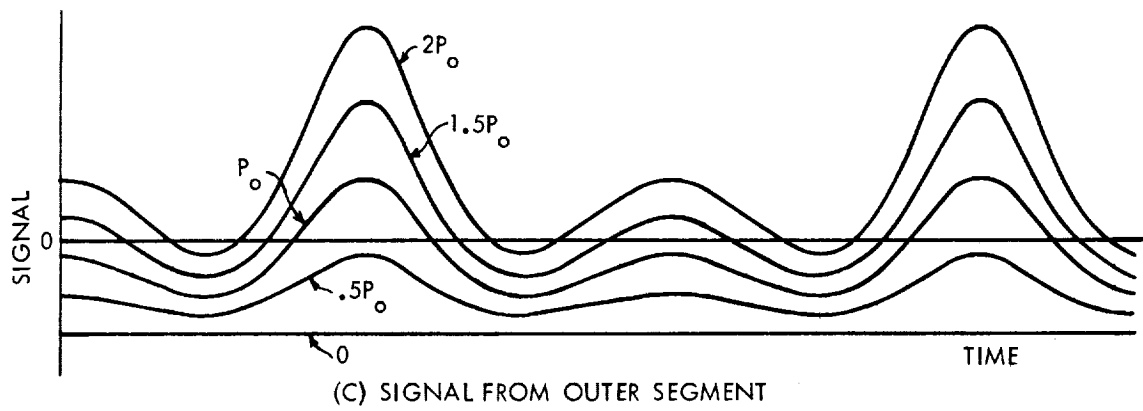
(C) SIGNAL FROM OUTER SEGMENT

(D) SIGNAL AFTER BIAS FEEDBACK

(E) OUTPUT SIGNAL FROM RECEPTOR

Figure 4.   Effect of Simultaneous Color Contrast

A) CURRENT DENSITY FOR AVERAGE INTENSITY

B) CURRENT DENSITIES FOR FIVE INTENSITIES
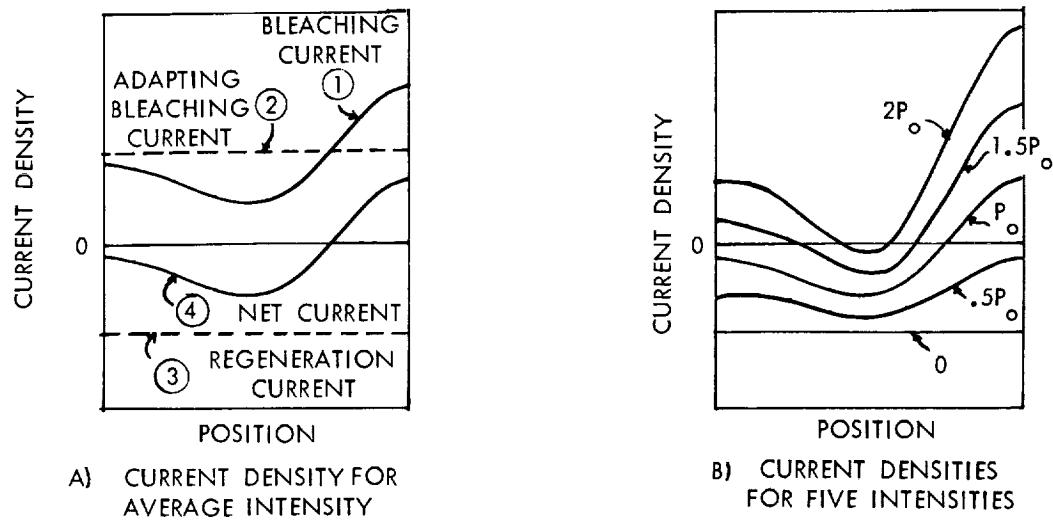
Figure 4. Effect of Simultaneous Color Contrast (continued)

signal from the summing network will be proportional to the curve for P_o. This average signal is fed back in the bias feedback loop. The effect is that a bias voltage is generated which is equal to the negative of the curve for P_o, and reduces the response to the P_o curve to zero. The signals after the bias feedback point are as shown in Diagram (D). The signal for intensity P_o is zero and that for zero intensity (the black object) is equal to the negative of the curve for P_o shown in Diagram (C).

The signals in Diagram (D) are amplified by the gain K_2. The output signal from the receptor is rectified and the rectified signals from the receptors are summed together to form an average rectified signal. If the gain K_2 were kept constant the average rectified signal would be proportional to the curve in Diagram (D) for 1.5 P_o. However, the fast gain control loop uses as a reference the average rectified signal, which is the response to the curve for 1.5 P_o, and controls the gain K_2 to make the response to the curve for 1.5 P_o a constant. The result is that the gain K_2 is reduced when the curve for 1.5 P_o rises, and vice versa, so that all the waveforms are effectively divided by the curve for 1.5 P_o. This results in stripping the modulation from all the waveforms, and so the output signals from the receptor are as shown in Diagram (E). These curves have no modulation components and consequently all the achromatic objects are seen i as achromatic.

Thus it has been shown how the basic control functions required to achieve achromatic adaptation in the receptors can also provide chromatic adaptation. These functions under normal conditions will make achromatic objects always appear achromatic, and, with regard to the achromatic scale, will keep white objects white and black objects black.

Helson[14] demonstrated the great effectiveness of the visual system is keeping achromatic objects achromatic. His experiments showed that, if the background illumination is a mixture of a monochromatic light and only 7 percent white light. achromatic

objects will appear achromatic. However, when the white light is reduced below that point, achromatic objects lighter than the background take on the color of the illuminant while achromatic objects darker than the background take on the color of the complement of the illuminant.

The result that Helson achieved with the extreme monochromatic illuminant is explainable by Figure 3. Diagram (E) shows that the current density for the average signal P_o has no spatial variation, that for brighter lights has the spatial variation of the illuminant and that for dimmer lights has the variation of the complement of the illuminant. These variations are normally eliminated by the gain control shown in Diagram (F). However, if the variations are too severe, which presumably occurs with extreme monochromatic illuminants, the gain variation can only partially compensate for the spatial variation of the illuminant, and so the observer sees achromatic objects as chromatic.

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SECTION 4

IMPLICATIONS OF CHROMATIC ADAPTION MODEL

The important point to draw from the preceding discussion
is that a straight-forward extension of the Spectral Scanning
theory leads one to the inescapable conclusion that the main
aspects of chromatic adaptation would be executed prior to the
demodulation processes that produce the trichromatic color
signals. In other words, chromatic adaptation would be performed,
not in terms of three-dimensional color data, but rather in terms
of the spectral patterns, defined by the spatial energy distribu-
tions and modulated waveforms, which have a much higher dimension-
ality. It is somewhat as if the visual system performed chro-
matic adaptation in terms of the spectra themselves.

Therefore, the Spectral Scanning theory is not a three
dimensional theory of color vision. The final color signal that
is generated is three dimensional, but the data processing
associated with chromatic adaptation, which has such a great
effect on what colors are actually seen, is implemented in terms
of data of much higher dimensionality. Thus this theory raises
a fundamental question concerning the validity of using three-
dimensional color matches as the basis for defining the color
vision process, particularly when one is trying to describe the
effects of adaptation.

The real issue is accuracy. The adaptation processes pro-
posed in the Spectral Scanning theory have a number of feedback
effects that keep the visual system in accurate calibration.
Direct comparisons between objects is made by the eye in terms
of the spatial energy distributions and the modulated waveforms,
which may be considered to be quasi-spectral data. These direct
comparisons yield the difference in the quasi-spectral data, and
it is this difference information that is demodulated to form
the trichromatic color signals. Consequently the system is

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capable of detecting in a reliable manner very small differences in spectra.

The purpose of a visual system is object identification, and so it is optimized to detect the reflectivity of an object, not the spectrum of the light emanating from it. The Spectral Scanning theory proposes that the visual system achieves this result by forming the reflectivity information directly in the optical detection process. The adaptation operation performed in the outer segment of the cone by the photopigment bleaching compensates for the effect of the illuminant spectrum (provided that the illuminant spectrum is the average spectrum to which the cone has become adapted) and therefore generates a current distribution that corresponds directly to the reflectivity of the object. The adaptation effect of the bleaching also tends to compensate for differences in the spectral characteristics of the individual cones, so that the signals generated in different cones by the same object are much more alike than are the static spectral characteristics of the separate cones.

By means of the adaptation effect achieved by photopigment bleaching, the visual system is able to detect very small amounts of chromaticity in the reflectivity characteristic of an object. An achromatic object will very accurately produce a d-c signal in each cone, and a slightly chromatic object will produce a slight but unmistakable a-c component. If there is no change of the relative spectrum from the average there is zero modulation on the signal generated in the outer segment of the cone; any change of the spectrum from the average produces modulation. Thus the visual system has inherent self regulation with respect to chromaticity, which allows it to adapt over a very large dynamic range and still achieve very high accuracy of chromaticity discrimination.

When the eye is viewing a natural image, the interactions of the signals from neighboring objects produces simultaneous

contrast effects. The spectral patterns from the objects, as represented by the modulated waveforms, are compared directly, and the differences between them are formed. It is the difference in the spectral pattern information that is actually demodulated to form the trichromatic signals. By working with differences in spectral patterns, the eye is able to detect very small differences in the chromaticity of neighboring objects. This gives rise to the enhancement in spectral resolution that is achieved by simultaneous contrast.

The preceding discussion shows how a visual system based on the Spectral Scanning theory could achieve very high fidelity in discriminating between objects of different reflectivity spectra and still be able to adapt to compensate for large variations in the intensity and chromaticity of illuminant. In contrast, it appears very doubtful that a visual system based on the Trichromatic theory could achieve anything approaching this high degree of performance.

The Trichromatic principle is employed in the design of color television cameras. In color television, the elements in the three camera channels are accurately matched to a precision that is certainly impossible to achieve with the flesh and blood components of the eye, and yet the color fidelity technically achievable in a color television system (ignoring economic considerations) does not ever compare with that of human vision. Besides, the instantaneous dynamic range of a color television camera is very low compared to the eye, and there is no mechanism in the optical detection itself (i.e., ignoring the effects of an iris of filter in front of the camera) that can allow it to adapt to different average levels of light. It is obvious that the eye cannot use component precision to achieve accuracy of spectral discrimination, as is employed in color television. Rather, the eye must rely on natural feedback processes. The author is unable to see how such feedback processes can be incorporated within the framework of the Trichromatic theory.

By processing the spectral information in a single channel (as predicted by the Spectral Scanning theory) the eye could achieve very accurate discrimination among objects having different reflectance spectra. An important consequence of this is that the spectral data processing would have a dimensionality much higher than three, and it is this much higher dimensionality that represents one of the basic mathematical differences between the Spectral Scanning theory and classical theories of color vision.

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SECTION 5

COMPARISON WITH CLASSICAL COLOR VISION THEORIES

The classical concept of the color vision receptor mechanism is based on the theory of Thomas Young[18] proposed in 1801. In essence, Young postulated that the eye has three different types of photosensitive elements with different spectral absorption curves, and the signals from these elements produce the neurological color information. Today this principle, with the multitude of extensions that have been built on it, is generally referred to as the Trichromatic theory. If we also include those theories that have generalized the Thomas Young principle by allowing four or more photosensitive elements, we find that essentially all theories of the receptor mechanism of color vision have been based on the Thomas Young principle.

The concensus of opinion today favors the Trichromatic concept that the receptor mechanism is defined by only three different spectral sensitivity curves. A strong argument for this point of view was presented by Hunt[15] in 1956, based on the phenomenon of constancy of metameric match. He reasoned that one can explain constancy of metameric match by assuming three photosensitive receptor elements with fixed spectral absorption curves. Spectra which match would evoke the same signals from each of these three elements, and so the spectra would always match regardless of how the signals from the photosensitive elements are processed. However, if there were four or more different types of photosensitive elements with independent spectral absorption curves, the responses of all these elements could not in general be the same for two matching spectra. Therefore if metameric matches were to be maintained, the sensitivities of the four or more separate channels would have to be interrelated in some precise and complicated manner, which seems unlikely.

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Hunt pointed out that it would be possible for the retina to have four or more different types of cones, provided the spectral responses of the curves can be expressed as linear algebraic sums of the responses of three basic spectral sensitivity curves. Thus we could allow four types of cones having different mixtures of three basic photopigments, where the absorption curves of the three photopigments would define the basic spectral response curves. It is of course also possible for the retina to have only one type of cone, which contains within it separate regions that define the three photosensitive elements. The important point is not the number of cones but rather the number of independent spectral absorption curves.

Therefore, if we accept the almost universally believed receptor principle of Thomas Young, we are apparently forced to accept the Trichromatic principle, that there are three and only three basic spectral response curves in the visual photodetection process. This is equivalent to requiring that the photodetection process be three dimensional. We thus have a very clear point of distinction between the Spectral Scanning theory and the classical approach to color vision. The classical approach leads to the conclusion that the photodetection process is three dimensional, whereas the Spectral Scanning theory leads to the conclusion that the photodetection process has a greater dimensionality.

If the optical detection process of the Spectral Scanning theory is more than three dimensional, how do we reconcile that theory with the argument made by Hunt with respect to constancy of metameric match. The answer is that the signal processing of the multi-dimensional data is performed within a single channel, and all that is required for constancy of metameric match is linearity within that channel. Hunt's arguments apply when we assume the color information is processed along three or more separate channels.

If the data processing in the receptor were exactly linear, it would make no difference what the dimensionality of the detection mechanism was. However, the data processing of the multi-dimensional spectral data proposed in the Spectral Scanning theory has important, though small, non-linearities, and these non-linearities are essential in the achievement of accurate spectral discrimination. Nevertheless, the non-linearities are sufficiently small under normal conditions for metameric matches to be approximately constant, which is in agreement with experiment.

The two major non-linearities in the signal processing performed in the receptor are the controlled gain variations in the outer and inner segments of the cone. A simple qualitative understanding of the non-linear effects produced by these gain variations can be obtained by approximating the response of the gain control process in the outer segment.

As a first approximation, assume as was shown in Figure 1 that the control varies the gain in the outer segment inversely with the regeneration current density R, which corresponds to the background (or time average illumination). The normalized signal X from the outer segment would then be

$$X = \frac{S - R}{R} = \frac{S}{R} - 1 \qquad (6)$$

where S is the current density produced by the sample. Express the sample and regeneration current densities S and R as sums of the average densities $\bar{S}$ and $\bar{B}$ plus the modulation components ΔS and ΔB. Equation 6, can then be written as

$$(1 + X) = \frac{S}{R} = \frac{\bar{S} + \Delta S}{\bar{R} + \Delta R} = \frac{\bar{S}(1 + \Delta S/\bar{S})}{\bar{R}(1 + \Delta R/\bar{R})} \qquad (7)$$

For convenience, the quantity (1 + X) is considered rather than X. The ratio of the peak value of the modulation deviation, to the

average value, is roughly proportional to the saturation of the light. Thus the peak value of $\Delta S/\overline{S}$ is roughly proportional to the saturation of the sample light, and the peak value of $\Delta R/\overline{R}$ is roughly proportional to the saturation of the background illumination. If the saturation of the background illumination is not excessive, $\Delta R/\overline{R}$ is much less than unity, and Eq. (7) can be approximated as

$$(1+X) \cong \frac{\overline{S}}{\overline{R}} \left[1 + \frac{\Delta S}{\overline{S}} \right] \left[1 - \frac{\Delta R}{\overline{R}} \right] = \frac{\overline{S}}{\overline{R}} \left[1 + \frac{\Delta S}{\overline{S}} - \frac{\Delta R}{\overline{R}} - \frac{\Delta S}{\overline{S}} \frac{\Delta R}{\overline{R}} \right] \quad (8)$$

The last term, $(\Delta S/\overline{S})(\Delta R/\overline{R})$ represents the non-linear effect in the gain control process. If the saturations of the background and sample lights are not both excessive, this non-linear effect is small.

Thus we would expect that non-linear effects would be small except under conditions of high saturation. When the lights are highly saturated we could expect there would be significant errors in metameric matches and in the operation of Grassman's laws. However, much more work is required before we can predict quantitatively how much errors would be expected.

If the two metamer spectra produced the same energy distributions across the cone there would be no change in the match regardless of non-linearities. However metamer spectra do not in general produce the same energy distributions across the cone. Nevertheless they do produce the same average value of energy distribution, because the luminosity signals for two metamer spectra must match (which is in accordance with Abney's law). This requirement that the d-c signals produced by metamer spectra are always equal regardless of non-linearities tends to minimize the effects of non-linearities in disturbing a metameric match.

Although the constancy of metameric matches is accepted as a solid foundation of color vision theory, there is little quantitative data to show how constant metameric matches actually are.

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One of the problems is that the eye has much less accuracy in making a metameric match of two unlike spectra than it has in detecting small differences between two spectral that are nearly alike. For this reason it is difficult to separate departures from linearity of metameric match from the natural randomness of metameric matches, even though those departures are very significant visually.

As an example, consider the color matching experiments being performed by Stiles[16] to develop a definition of the standard observer for a 10-degree field of view. The standard deviations of the settings of each primary is of the order of 10 percent for the group of observers, and 3 percent for a single observer, when the primary is relatively large. When a primary is small the standard deviation of its setting may be as large as 80 percent for the group of observers. When this deviation data is related to the resultant accuracy of the chromaticity diagram, the author found a maximum error of about ± 6 percent in x and y for the group of observers and nearly ± 2 percent for the single observer, occurring roughly at 500mμ.*

In contrast, the tolerance set on Munsell chips corresponds to ± 0.2 Munsell chroma, and the commercial tolerances for wool dyes is typically about ± 0.4 Munsell chroma.[13] These tolerances correspond to x or y deviations in the CIE chromaticity diagram of about ± 1/3 percent and ± 2/3 percent for value 6 in the vicinity of illuminant C. The best match that can be made spectrally corresponds to less than ± 0.1 percent in x or y. For this reason the CIE chromaticity coordinates are specified to four significant figures, even though the metameric matches from which it is derived do not have anywhere near that accuracy.

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*These represent ± 2 σ, where σ is the standard deviation. If the standard deviations σ for x and y are equal, there is a 90 percent probability that the measured point on the chromaticity diagram will lie within ± 2σ of the specified x and y values.

Thus, a color vision theory could allow significant percentage errors in metameric matches and Grassman's laws and still be in agreement with visual experiment. After all, there is no need for the eye to satisfy metameric matches with high accuracy. Rather, what the eye must be able to do is achieve high accuracy in the comparison of similar spectra. In addition, it should have high accuracy in maintaining constancy of color of natural objects independent of changes of illumination.

When we consider the problem of constancy of object color we enter the area of chromatic adaptation. An excellent summary of the present status of visual adaptation has been presented by Stiles.[17] Metameric matches merely define equivalence classes between spectra; they say nothing about what color sensation the spectra evoke. Although the techniques for dealing with metameric matches are highly refined, the psychophysical description of chromatic adaption is still in its infancy. Various color matching experiments have been performed to yield a quantitative description of chromatic adaptation, but they have encountered two major difficulties:

(1) The measured data has a randomness much greater than that in standard color matching experiments.

(2) There appears to be a great complexity in the underlying relationships between color sensation and adaptation conditions.

These experiments are usually made by means of binocular matching. However memory matching and the differential adaptation of different parts of the eye have also been employed.

An important implication of the Spectral Scanning theory is that it provides a new approach to the problem of chromatic adaptation. The theory suggests that the apparent randomness and complexity observed in the chromatic adaptation experiments is the result of our attempt to define the multi-dimensional adaptation process in terms of three dimensional color matching experiments. The Spectral Scanning theory proposes that the eye

is achieving high accuracy of chromatic adaptation in a simple manner by performing the adaptation in terms of the multi-dimensional spectral patterns generated by the waveguide mode effects. However this inherent accuracy and simplicity appears as randomness and complexity when we measure the multi-dimensional chromatic adaptation phenomenon by means of three dimensional color matching experiments. Rather we must study the chromatic adaptation phenomena more in terms of the spectra themselves.

Our attempts to define the multi-dimensional chromatic adaptation process in terms of three dimensional color matching experiments may be likened to the proverbial two-dimensional man in Flat Land trying to interpret his experiences of the three dimensional world. Our two-dimensional man can observe a three-dimensional object only in terms of the cross section of the object lying within the plane of Flat Land. When a three-dimensional object passes through Flat Land, our two-dimensional man encounters a phenomenon of great complexity as he observes the varying shape of the cross section of the object lying within his plane, even though the three-dimensional object is very simple.

An important practical problem that is struggled with in the field of color standardization is that of defining a uniform color space. Very tedious emperical studies are being performed to improve our present color mapping techniques. However, since there are 10 million separately distinguishable colors, the problem is tremendous. A theory that could provide a better framework for color standardization by explaining the observed anomolies in color space would be very valuable. If we extend the Spectral Scanning theory by defining in precise terms the multi-dimensional manner in which chromatic adaptation is con-sidered to be performed, we may well achieve a simple theoretical model that can accurately predict the apparently complex relation-ships of color space.

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